TRANSACTIONS

OF

THE LINNEAN SOCIETY.

I. *On the Development of the Ovulum in* Avicennia. *By the late* William Griffith, *Esq., F.L.S. &c. &c. Communicated by* R. H. Solly, *Esq., F.R.S., L.S. &c. &c.*

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In connexion with the development of the seed and embryo in *Santalum* and *Osyris*, the following account of the development of the same parts in *Avicennia* may not be altogether misplaced; for the placentation is almost precisely the same; the same posterior elongation of the embryo-sac takes place; and in all the embryo is, at least when matured, external to the nucleus or body of the ovulum.

The ovula of *Avicennia* appear to me to be nucleary: they closely resemble in appearance the same bodies in *Santalum*, *Osyris*, *Schœpfia*, *Olax*, *Congea*, &c. (Tab. I. figs. 1, 2.)

The first change observed takes place in the central tissue of the ovulum, which appears to become of a denser nature than the rest, the density gradually extending to near the apex of the ovulum, in which, at a period antecedent to fecundation, the embryo-sac will be found. This embryo-sac appeared in most instances to be a membranous sac with an enlarged apex or head, contained within the apex of the nucleus, and a subcylindrical body, extending backwards a short way to the termination of the dense central tissue, into which at this period a vascular fascicle is seen to be extended (Tab. I. figs. 3, 4.).

The first change, subsequent to the application of the pollen-tubes to the apex of the sac, appeared to consist of the usual preparatory steps in the formation of cellular tissue (TAB. I. fig. 5.).

The next change observed was one affecting the figure of the sac itself, which now exhibited, as it were, a short prolongation posteriorly in the direction of the axis of the ovulum, and consequently in exact relation with the dense central tissue; or, in other words, instead of being straight, it now appeared curved at its anterior extremity. The subcylindrical body of the sac was also observed to have become prolonged posteriorly within the inner side of the ovulum (TAB. I. figs. 6, 7.).

That half of the dilated head of the embryo-sac next the short central prolongation was at this period observed to be filled with rudimentary cellular tissue or young albumen. As this albuminous tissue increases, it first occupies the whole of the original head of the sac, which then appears to become enlarged, and then to pass out of the apex of the ovulum (TAB. I. figs. 8, 9.), to which direction its subsequent enlargement is almost entirely confined. At the same time the posterior prolongation of the body of the sac continues. The albuminous tissue having attained some size, will be found to present towards its centre, and corresponding with the axis of the ovulum and that of the application of the pollen-tubes, the rudiments of the future embryo (TAB. I. fig. 9.).

At a subsequent period the albuminous mass, being considerably increased in size, presented on its anterior surface a curved furrow or groove, which was found to correspond with the points of the cotyledons of the young embryo, now considerably increased in size (TAB. I. figs. 11, 12.). At this period the part of the sac within the ovulum has undergone little change, except the posterior (lateral) prolongation, which has by this time passed back into the placenta, within which it is divided in a digitate irregular manner (TAB. I. fig. 10.).

The next stage presented the points of the cotyledons quite naked (*i. e.* external to any part of the seed), they having protruded through the groove above mentioned. As the embryo increases in size the cotyledons become more and more exposed: the part of the albumen below the line of exsertion of the cotyledons does not undergo much change; but that part above the

same line, or rather between the inner cotyledon and body of the ovulum, becomes enlarged and flattened almost into a membrane; and even when the cotyledons are as long as the placenta, this part of the albuminous tissue equals them in length (Tab. I. fig. 13.).

The mature embryo, with the exception of its radicle, which is always imbedded in the albuminous tissue, may be said to be naked. The upper part of the albumen at this period is much dilated, and almost membranous; the edges are very irregular (Tab. I. figs. 13 & 14.).

The conduplication of the cotyledons takes place at an early period; their inequality at a much earlier, even before the protrusion of their points.

The central prolongation of the sac was not observed later than the period represented by fig. 12. Tab. I., but it is probable from appearances that it is at length filled with albuminous tissue.

The exact distance to which the vascular fascicle at length reaches was not observed: probably it extends, when complete, to the apex of the short central prolongation of the sac.

The above observations were made very shortly before my departure from Malacca: they are deficient in several respects; but of the mode by which the embryo becomes external to the seed to so great a degree I can speak with the requisite confidence.

I now proceed to offer my remarks on the circumstances detailed above.

The elongation of the posterior end of the embryo-sac, occurring as it does in a plant so different in general organization from those in which it has hitherto been observed, appears to me remarkable. It is curious that this prolongation has only been observed in association with a particular form of the free central placenta, and thus the exact observation of the corresponding developments in *Olax* and *Congea* becomes more desirable than ever.

The shape of the embryo-sac in that stage, represented by fig. 7. Tab. I., is also worthy of notice: so far as I know, it is the only instance of an embryo-sac prolonged posteriorly, it may be said, from two points of its surface, or which may not be considered to be in itself a rectilinear body. The general analogy of the relations of the embryo-sac with the nucleus would lead me to suppose that the embryo-sac of *Avicennia* consisted originally of that part in the axis of the ovulum, viz. the head or dilated end, and what I

have called the short central prolongation. But what has been recorded of *Santalaceæ* (and the whole of my observations on *Avicennia*) is opposed to this; for in all the instances observed, the posterior prolongation is a prolongation of the posterior end of the sac itself, which obviously would not be the case if the ordinary relations of embryo-sacs to their nuclei existed in *Avicennia*.

Another non-analogous instance may be observed in the gradual protrusion outwards of the young albumen, which is assumable as being at one period entirely interior to the nucleus or ovulum. In all the really analogous instances in which the albumen is exterior to the ovulum, it is *always* exterior, that part of the embryo-sac in which it is developed being protruded long before any albuminous tissue has been developed, which indeed is almost always subsequent to fecundation properly speaking, viz. the completion of certain relations between the anterior end of the pollen-tube and the embryo-sac.

A third non-analogous instance seems to me presented by the exsertion or protrusion of the cotyledons. Protrusion of the radicular end of the embryo is not, perhaps, uncommon; but in these cases it may be difficult to ascertain to what extent the protrusion may be due to germination.

In *Cryptocoryne ciliata* (*Ambrosinia ciliata*, Roxb.) however the protrusion takes place long before the cotyledon has acquired its full growth, up to which period moreover it retains its firm fleshy substance. In a Malacca subgeneric form of *Cryptocoryne*, in which the margins of the spatha cohere into a tube to a great extent, although the plumula is still of considerable size, no protrusion whatever takes place. By the peculiar way in which this is performed the embryo becomes almost entirely naked, without however changing the direction it would have had, had it been developed, as it so generally is, within the body of the seed. It is curious that the obliquity in the direction of the young embryo, which is still more extraordinary, takes place at a very early period, for it forms an obtuse angle with the line of the axis of the ovulum and application of the pollen-tubes before there is any indication of cotyledons. For this I do not see any appreciable reason, mechanical or otherwise, though it would perhaps be amiss to overlook the comparative density of the axis of the ovulum in endeavouring to account for the protrusion of

the albumen, and perhaps for the production of the lateral posterior prolongation.

The extension of the vascular fascicle so far into what has been considered the ovulum, leads me to doubt the real extent of this organ. I cannot recall to mind any instance in which the vascular supply of the ovulum is prolonged into the substance of the nucleus. A similar doubt is suggested by the extent of the head of the embryo-sac inside the ovulum; for this sac in general, during the development of the albumen and embryo, is made gradually to encroach upon the nucleus, by which this originally solid cellular body becomes generally reduced to a mere cellular membranous covering, or possibly to be entirely obliterated. But whatever may be the real extent of the ovulum, the nucleary form of which is only physiologically distinguishable from the placenta, the co-existence of a vascular fascicle with the posterior prolongation in *Avicennia* seems to me to be against the opinion of these curious extensions being of a chalazal nature.

I was not able to ascertain clearly the absolute relations with the embryo-sac established by the pollen-tube after it had reached the sac, still less the absolute relations which the end of the pollen-tube bore to the nascent embryo. All the indications however furnished by my sketches are in favour of the penetration of the pollen-tube into the sac, as far as the spot in which the embryo makes its first appearance.

Attention to a peculiarity between the direction of the unimpregnated ovulum and that of the seed in *Avicennia* was first pointed out by Mr. Brown in his 'Prodromus*,' in which it is ascribed to the fecundated ovulum becoming erect. This would manifestly make the radicle superior; but if the ovulum were of the same nature as in *Myoporinæ*, to which Mr. Brown's remarks seem to refer, it would as obviously make the radicle inferior. In a subsequent account given by Mr. Brown through Dr. Wallich†, the erection of the seed is attributed to an elongation upwards of the body of the seed, the (true) apex maintaining its original (inferior) situation.

The most important difference between this last account and that which I have attempted to give, is, that I find *the embryo only* to be erect; one part of the ovulum (the nucleus), from which it is assumable the seed-coat might

* *Op. cit.*, ed. Nees, p. 374. † Pl. Asiat. Rar. iii. pp. 44, 45.

have been, partly at least, derived, suffering no change in direction whatever, and the other, from which the albuminous covering might have equally resulted, only a partial one. The embryo also, in its earlier stages of development, undergoes a degree of change of direction, but only sufficient to enable it to pass up outside the ovulum, in the same direction it would have maintained had it been ordinarily developed.

EXPLANATION OF THE PLATE.

TAB. I.

Avicennia resinifera, Forst. fide Jack, and *Av. intermedia*, Griff. MSS.*

Fig. 1. Placenta and ovula, at an early period before expansion of flower, and before the corolla exceeds the calyx in length (species not noted).

Fig. 2. Longitudinal section of one of the ovula of the same; the subsequent dense central tissue appears to be commenced.

Fig. 3. Longitudinal section of an ovulum, more advanced; the apex of the embryo-sac is close to the apex of the ovulum, and its body cylindrical, reaching to the central dense tissue (*A. resinifera*).

Fig. 4. Embryo-sac of the same, separated.

Fig. 5. Embryo-sac of an ovulum at the period after the application of the pollen-tubes to its apex:—magnified about 500 times (*A. resinifera*).

Fig. 6. Longitudinal section of an ovulum of the same after blackening of the apex of the style, the fall of the corolla, and evident enlargement of the ovarium; part of a pollen-tube is seen attached. The embryo-sac is enlarged, and extends further posteriorly; otherwise there is little change in the ovulum.

Fig. 7. Longitudinal section of an ovulum, a little more advanced. The embryo-sac is more prolonged posteriorly, and also presents a short prolongation corresponding with the axis of the ovulum. It is still interior to the ovulum; the dilated apex has commenced to be cellular.

Fig. 8. Placenta and ovula (*A. intermedia*) at a more advanced stage: three of the ovula have aborted; the fertilized one is seen laterally, and a protuberance (*a*) is visible from its apex.

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* *A. intermedia* is founded on a Malacca plant altogether intermediate between what appears to be *A. tomentosa* and *A. resinifera*.

Fig. 9. Longitudinal section of an ovulum of this period: the young albuminous mass (the protuberance of fig. 8.) is now seen to be partly exterior to the ovulum. A pollen-tube is still in attachment. The disc represents the rudimentary embryo.

Fig. 10. Part of the ovulum, the whole of the posterior lateral elongation, now digitate at the end, which is confined in the placenta, and once-branched also within the ovulum, the central or axile prolongation, the now almost entirely exserted albumen, and the embryo. This figure does not represent a section of the albuminous mass, but of the body of the ovulum alone, one side of which was sliced off to expose the albumen.

Fig. 11. Placenta (entire) of an ovarium some time after fecundation. *a.* Apex of the placenta. *b, b.* Barren ovula. *c.* Fecundated ovulum. *d.* Exserted albuminous mass, showing the furrow or chink? by which the points of the cotyledons will pass out (*A. intermedia*).

Fig. 12. Fecundated ovulum; longitudinal section through the body of the nucleus, but not through the albuminous mass: the tips of the cotyledons reach the furrow or chink.

Fig. 13. An entire placenta of *A. resinifera* at a more advanced period: the letters have the same references; *e.* shows the lower edge of the former furrow, now an opening; *d.* the large inner lip or edge with irregular margins overlapping the cotyledons.

Fig. 14. Young seed and embryo about the same period of development: the embryo is removed from the seed, which is viewed obliquely. *a.* Body of the ovulum or nucleus. *b.* Fleshy part of the exserted albuminous mass. *c.* Lower or outer edge of the fissure by which the cotyledons have protruded. *d.* Inner or upper, now membranous, cellular edge of the same.